ANNALS
of CARNEGIE MUSEUM

CARNEGIE MUSEUM OF NATURAL HISTORY

INTRAISLAND AND INTERISLAND VARIATION IN ANTILLEAN POPULATIONS OF *MOLOSSUS MOLOSSUS* (MAMMALIA: MOLOSSIDAE)

HUGH H. GENOWAYS
Curator, Section of Mammals

ROBERT C. DOWLER[1]

CATHERINE H. CARTER[2]

ABSTRACT

Significant levels of secondary sexual variation and expected levels of individual variation were demonstrated in all samples of *Molossus molossus* from Jamaica, Guadeloupe, and Trinidad examined with univariate analyses. Significant morphometric differences were demonstrated among samples of *Molossus molossus* that originated from geographically close localities on the same island. Using multivariate techniques, broader patterns of geographic variation were demonstrated among the Antillean populations of *M. molossus*.

INTRODUCTION

The small members of the genus *Molossus* with pale-based hair occur throughout the Antilles and in adjacent areas of northern South America and Middle America. Recent authors (Husson, 1978; Jones

[1] Address: Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843.
[2] Address: Mississippi Museum of Natural Science, 111 North Jefferson Street, Jackson, MS 39202.

et al., 1971; Koopman, 1978; Varona, 1974) have considered these populations as a single species *(Molossus molossus)*, whereas earlier authors (Miller, 1913; Hall and Kelson, 1959) have judged there to be as many as 10 species in this group.

These bats are badly in need of taxonomic revision. Earlier workers were confused by the high degree of local variation as well as geographic and secondary sexual variation. Jones et al. (1971) hypothesized that because populations were highly localized and presumably inbred, they may diverge morphologically "to a degree that mensural differences can be demonstrated even between samples from the same general geographic area." The presence of these localized populations may be at least partially responsible for the many names assigned to this group. The recently described subspecies *lambi* (Gardner, 1966) may be an example of such a local population.

Having samples of *Molossus molossus* available from the islands of Jamaica, Guadeloupe, and Trinidad in the Antilles led us to examine the degree of local as compared to geographic variation. Islands present an ideal situation for making these comparisons. Because populations on an island are potentially members of the same breeding population, demonstrable mensural differences among intraisland samples would indicate that these bats are exhibiting an unusual degree of local variation, possibly by forming local breeding demes. Presumably there is no opportunity for interbreeding among populations on widely separated islands in the Antilles; therefore, we would expect a greater variation among populations on different islands than among populations on the same island.

This paper should be viewed as the first phase of a study to clarify the systematic relationships of the small-sized members of the genus *Molossus*. The hypotheses that are tested in this study are: (1) there is no significant variation among intraisland populations of *Molossus molossus* and (2) the amount of interisland variation exceeds the amount of intraisland variation. An assessment of the amount of intraisland as compared to interisland variation should be important to future studies of geographic variation in this group, especially when mainland populations are studied.

We have not used subspecific names throughout this paper because of the taxonomic uncertainty in this group and because they are not necessary for the current study. However, currently the name *M. m. milleri* would apply to populations from Jamaica and *M. m. molossus* to populations from Guadeloupe and Trinidad (Hall, 1981:255–257).

METHODS AND MATERIALS

From all specimens, one external and nine cranial measurements were recorded. All measurements are given in millimeters and were taken by means of dial calipers as

follows: *length of forearm*, from posteriormost projection of the elbow to the anterior-most projecting portion of wrist joint with wing flexed; *greatest length of skull*, distance from posteriormost projection of the cranium to anteriormost surface of the upper incisors; *condylobasal length*, distance from posteriormost projection of exoccipital condyles to anteriormost projection of premaxillae; *zygomatic breadth*, greatest width across zygomatic arches at right angle to longitudinal axis of cranium; *mastoid breadth*, greatest width across mastoid processes, at right angle to longitudinal axis of skull; *breadth of braincase*, greatest width across braincase at widest point, at right angle to longitudinal axis of skull; *postorbital constriction*, least width across the postorbital constriction, at right angle to the longitudinal axis of cranium; *length of maxillary tooth-row*, distance from posterior lip of alveolus of M³ to anterior lip of alveolus of canine; *breadth across upper molars*, greatest distance from labial margins of upper molars at the widest point; *length of mandibular toothrow*, distance from posterior lip of alveolus of M³ to anterior lip of alveolus of canine.

Only adult specimens (all specimens deposited in collection of The Museum, Texas Tech University) with phalangeal epiphyses completely fused were used in this study. Specimens were grouped into seven samples as follows for analysis: *Sample 1*—TRINIDAD: Blanchisseuse; Las Cuevas. *Sample 2*—TRINIDAD: Maracus Valley; Port of Spain; San Rafael. *Sample 3*—GUADELOUPE: 2 km N Ballif, Basse-Terre; 1 km S Basse-Terre, Basse-Terre. *Sample 4*—GUADELOUPE: 1 km N, 1 km W St. François, Grand-Terre. *Sample 5*—JAMAICA: Duanvale, Trelawny Parish. *Sample 6*—JAMAICA: ½ mi S, ½ mi W Runaway Bay, St. Ann Parish. *Sample 7*—JAMAICA: Queenhythe, St. Ann Parish.

Statistical procedures were performed on the IBM 370 computer at Texas Tech University. The univariate program yielded standard statistics (mean, range, standard deviations, standard error of the mean, variance, and coefficient of variation) and employed a single-classification analysis of variance (F-test, significance level 0.05) to test for significant differences between or among means (Sokal and Rohlf, 1969). When means were found to be significantly different, the Sum of Squares Simultaneous Test Procedure (SS-STP) was used to determine maximally nonsignificant subsets (Gabriel, 1964).

Cluster and principal component analyses were performed on standardized data using the NT-SYS program. A matrix of phenetic distance coefficients was computed and a cluster analysis was conducted using UPGMA (unweighted pair-groups method using arithmetic averages) on this matrix. The phenogram generated by the cluster analysis was compared with the original matrix, and a coefficient of cophenetic correlation was computed. A matrix of Pearson's product-moment correlation among characters was computed, and the first three principal components extracted. Projections of the OTUs onto the first three principal components were made.

Additional multivariate analyses were performed using the Statistical Analysis System (SAS) package developed by Barr and Goodnight (Service, 1972). A multivariate analysis of variance (MANOVA) and canonical analysis were performed to determine the degree of divergence among samples. Canonical analysis of data provides weighted combinations of characters, which maximizes the distinction among groups. This analysis extracts characteristic roots and vectors and computes a mean canonical variate for each sample. Additional orthogonal axes are constructed, which extract the next best combination of characters. This analysis emphasized those characters with the least within sample and greatest among sample variation, hence, providing the best combinations of characters to discriminate among samples. Each eigenvalue and its corresponding canonical variate represents an identifiable fraction of the total variation. Sample means and individuals were plotted on the first three canonical variates. The relative importance of each original variable to the first two canonical variates was computed. These techniques have recently been used in the study of mammals by Schmidly and Hendricks (1976), Yates and Schmidly (1977), and Swanepoel and Genoways (1978).

Results

Univariate Analyses

Secondary sexual and individual variation were assessed in order to understand these two types of non-geographic variation in Antillean populations of *Molossus molossus*. Intraisland and interisland variation were also examined to determine if significant variation was present.

Secondary sexual variation.—Males and females from each sample were compared to determine the amount of secondary sexual variation present (Table 1). Two or more samples were significantly different for all measurements. Length of forearm exhibited the least amount of secondary sexual variation with only the two samples from Guadeloupe showing significant variation. Postorbital constriction revealed significant secondary sexual variation in only three samples (3, 4, and 7). In three measurements (greatest length of skull, condylobasal length, and mastoid breadth), the sexes were significantly different for all seven samples. Only one sample (5) did not show significant secondary sexual variation for zygomatic breadth and only two samples did not differ significantly for breadth across upper molars (1 and 7) and length of mandibular toothrow (2 and 5).

The greatest amount of secondary sexual variation was exhibited by the two samples from Guadeloupe. Males and females differed in all measurements for sample 3 and all but breadth of braincase for sample 4. Samples 1 and 5 revealed the least amount of secondary sexual variation differing in only five measurements.

In all subsequent analyses, males and females have been handled separately.

Individual variation.—The amount of individual variation present in these samples is small, indicating that each probably represents a single population (Table 1). Highest coefficients of variation for males were recorded for postorbital constriction in sample 4 (7.7) and mastoid breadth in sample 5 (4.2), whereas for females highest values were for length of maxillary toothrow in sample 6 (5.8) and postorbital constriction in sample 1 (5.5). Generally, amount of individual variation was comparable between the sexes and among the seven samples.

Intraisland variation.—Males and females were compared separately from two samples from Guadeloupe (3 and 4) and the three from Jamaica (5–7) to determine if significant differences occur between or among samples from a single island (Table 1). The samples from Trinidad were not considered in this portion of the analyses because these samples were formed by grouping material from adjacent localities.

Table 1.—*Variation in external and cranial measurements of* Molossus molossus *from Jamaica, Guadeloupe, and Trinidad. Samples are defined in text.*

Sample	Sample size	Mean	(Range)	±2 SE	CV
			Males		
Length of forearm					
1	4	38.1	(36.8–39.3)	±1.10	2.9
2	11	37.4	(36.7–38.4)	±0.37	1.6
3	23	38.7	(37.8–40.3)	±0.27	1.7
4	20	38.9	(37.1–40.7)	±0.40	2.3
5	3	38.8	(38.6–39.2)	±0.40	0.9
6	9	39.0	(38.3–39.8)	±0.31	1.2
7	24	39.0	(38.0–40.3)	±0.24	1.5
Greatest length of skull					
1	4	17.6	(17.4–17.7)	±0.13	0.7
2	11	17.3	(16.6–17.7)	±0.22	2.1
3	23	17.0	(16.4–17.4)	±0.11	1.5
4	20	17.0	(16.1–17.7)	±0.19	2.5
5	3	17.8	(17.8–17.9)	±0.07	0.3
6	9	17.3	(16.8–17.5)	±0.17	1.4
7	24	17.8	(17.2–18.5)	±0.13	1.8
Condylobasal length					
1	4	17.0	(16.8–17.3)	±0.22	1.3
2	11	16.7	(16.3–17.3)	±0.17	1.7
3	23	16.5	(15.9–17.1)	±0.11	1.6
4	20	16.5	(15.7–17.4)	±0.19	2.5
5	3	17.4	(17.1–17.8)	±0.43	2.2
6	9	17.0	(16.7–17.3)	±0.14	1.2
7	24	17.3	(16.8–17.5)	±0.22	2.1
Zygomatic breadth					
1	4	10.9	(10.4–11.0)	±0.30	2.8
2	11	10.7	(10.3–11.0)	±0.15	2.3
3	23	10.6	(10.3–10.8)	±0.06	1.4
4	20	10.8	(10.2–11.0)	±0.10	2.1
5	3	10.7	(10.2–11.1)	±0.52	4.2
6	9	11.1	(10.8–11.4)	±0.11	1.5
7	24	11.0	(10.7–11.4)	±0.08	1.8
Postorbital constriction					
1	4	3.7	(3.6–3.8)	±0.10	2.6
2	11	3.6	(3.4–3.9)	±0.09	3.9
3	23	3.4	(3.2–3.7)	±0.05	3.5
4	20	3.7	(3.4–4.8)	±0.13	7.7
5	3	4.0	(3.9–4.0)	±0.07	1.5
6	9	4.1	(4.0–4.2)	±0.05	1.8
7	24	4.1	(3.9–4.4)	±0.05	2.9

Table 1.—*Continued.*

Sample	Sample size	Mean	(Range)	±2 SE	CV
Breadth of braincase					
1	4	8.9	(8.7–9.1)	±0.16	1.8
2	11	8.9	(8.5–9.3)	±0.14	2.7
3	23	8.6	(8.4–8.9)	±0.05	1.5
4	20	8.7	(8.4–9.0)	±0.08	2.0
5	3	9.0	(8.9–9.1)	±0.12	1.1
6	9	8.9	(8.7–9.1)	±0.09	1.6
7	24	9.0	(8.6–9.9)	±0.10	2.8
Mastoid breadth					
1	4	10.4	(10.2–10.8)	±0.28	2.7
2	11	10.2	(10.0–10.5)	±0.10	1.6
3	23	10.2	(9.6–10.6)	±0.11	2.5
4	20	10.3	(9.9–10.6)	±0.10	2.2
5	3	10.7	(10.2–11.0)	±0.52	4.2
6	9	10.8	(10.5–11.1)	±0.14	1.9
7	24	10.7	(10.2–11.1)	±0.09	2.0
Length of maxillary toothrow					
1	4	6.0	(5.9–6.1)	±0.10	1.6
2	11	5.9	(5.6–6.1)	±0.08	2.3
3	23	5.7	(5.3–6.4)	±0.10	4.2
4	20	5.8	(5.5–6.2)	±0.08	3.3
5	3	5.7	(5.7–5.8)	±0.07	1.0
6	9	6.0	(5.8–6.4)	±0.12	3.0
7	24	5.9	(5.6–6.2)	±0.07	2.8
Breadth across upper molars					
1	4	7.7	(7.3–8.0)	±0.29	3.8
2	11	7.9	(7.6–8.2)	±0.13	2.7
3	23	7.7	(7.4–8.0)	±0.06	2.0
4	20	7.7	(7.3–8.2)	±0.11	3.2
5	3	8.0	(7.9–8.0)	±0.07	0.7
6	9	7.9	(7.7–8.0)	±0.07	1.3
7	24	7.9	(7.5–8.2)	±0.07	2.3
Length of mandibular toothrow					
1	4	6.7	(6.6–6.9)	±0.15	2.2
2	11	6.6	(6.3–7.0)	±0.15	3.6
3	23	6.4	(6.2–6.7)	±0.05	2.0
4	20	6.5	(5.9–6.7)	±0.08	2.8
5	3	6.7	(6.6–6.7)	±0.07	0.9
6	9	6.7	(6.5–6.9)	±0.09	2.0
7	24	6.7	(6.5–7.0)	±0.05	1.9
Length of forearm					
1	5	37.8	(36.6–38.8)	±0.74	2.2
2	15	37.8	(35.4–40.2)	±0.62	3.2
3	22	38.1	(36.1–39.3)	±0.34	2.1
4	20	37.9	(36.0–38.9)	±0.32	1.9
5	10	38.7	(38.1–40.3)	±0.40	1.6
6	10	38.5	(37.4–39.0)	±0.33	1.4
7	22	38.7	(37.3–40.2)	±0.31	1.9

Table 1.—*Continued.*

Sample	Sample size	Mean	(Range)	±2 SE	CV
Greatest length of skull					
1	5	16.5	(16.2–16.6)	±0.14	0.9
2	16	16.5	(15.9–17.3)	±0.17	2.0
3	22	16.1	(15.5–16.5)	±0.12	1.7
4	20	16.3	(15.8–17.0)	±0.13	1.7
5	10	16.8	(16.3–17.1)	±0.15	1.4
6	10	16.7	(16.5–16.9)	±0.09	0.9
7	22	16.9	(16.3–17.6)	±0.12	1.7
Condylobasal length					
1	5	15.9	(15.7–16.0)	±0.12	0.8
2	16	16.0	(15.5–16.6)	±0.16	1.9
3	22	15.7	(14.8–16.0)	±0.13	2.0
4	20	15.9	(15.4–16.7)	±0.14	2.0
5	10	16.4	(16.3–16.7)	±0.13	1.3
6	10	16.5	(16.3–16.7)	±0.08	0.8
7	22	16.5	(16.0–16.9)	±0.09	1.3
Zygomatic breadth					
1	5	10.2	(10.0–10.4)	±0.15	1.6
2	16	10.2	(9.9–10.6)	±0.10	2.0
3	22	10.1	(9.7–10.4)	±0.08	1.8
4	20	10.3	(9.9–10.9)	±0.10	2.1
5	10	10.6	(10.4–10.9)	±0.10	1.5
6	10	10.6	(10.3–10.8)	±0.09	1.4
7	22	10.6	(10.3–10.9)	±0.06	1.3
Postorbital constriction					
1	5	3.5	(3.2–3.7)	±0.17	5.5
2	16	3.5	(3.3–3.8)	±0.06	3.3
3	22	3.4	(3.1–3.5)	±0.04	3.1
4	20	3.3	(3.2–3.7)	±0.04	2.9
5	10	4.0	(3.9–4.1)	±0.04	1.7
6	10	4.0	(3.8–4.1)	±0.06	2.3
7	22	4.0	(3.8–4.1)	±0.03	2.0
Breadth of braincase					
1	5	8.9	(8.6–9.4)	±0.28	3.5
2	16	8.5	(8.1–8.8)	±0.09	2.2
3	22	8.4	(8.1–8.6)	±0.06	1.7
4	20	8.5	(8.2–8.9)	±0.08	2.0
5	10	8.8	(8.6–8.9)	±0.05	1.0
6	10	8.8	(8.5–9.8)	±0.24	4.4
7	22	8.7	(8.5–9.0)	±0.05	1.3
Mastoid breadth					
1	5	9.7	(9.6–10.0)	±0.15	1.7
2	16	9.8	(9.2–10.2)	±0.13	2.7
3	22	9.6	(8.2–10.0)	±0.16	3.9
4	20	9.8	(9.4–10.3)	±0.10	2.2
5	10	10.3	(10.0–10.4)	±0.08	1.3
6	10	10.3	(10.0–10.5)	±0.10	1.5
7	22	10.3	(9.9–10.6)	±0.07	1.6

Table 1.—*Continued.*

Sample	Sample size	Mean	(Range)	±2 SE	CV
Length of maxillary toothrow					
1	5	5.7	(5.5–5.8)	±0.12	2.3
2	16	5.7	(5.4–6.2)	±0.09	3.1
3	22	5.5	(5.3–5.9)	±0.06	2.4
4	20	5.5	(4.7–5.8)	±0.07	4.4
5	10	5.6	(5.5–5.8)	±0.07	2.1
6	10	5.8	(5.6–6.7)	±0.21	5.8
7	22	5.7	(5.5–5.9)	±0.05	2.3
Breadth across upper molars					
1	5	7.6	(7.5–7.8)	±0.12	1.7
2	16	7.5	(7.2–8.2)	±0.13	3.3
3	22	7.4	(7.2–7.6)	±0.06	1.9
4	20	7.4	(7.0–7.7)	±0.09	2.9
5	10	7.7	(7.5–7.9)	±0.11	2.2
6	10	7.6	(7.3–7.9)	±0.11	2.3
7	22	7.8	(7.4–8.9)	±0.15	4.6
Length of mandibular toothrow					
1	5	6.4	(6.2–6.5)	±0.12	2.0
2	16	6.5	(6.2–7.0)	±0.10	3.2
3	22	6.2	(6.0–6.4)	±0.05	1.9
4	20	6.3	(6.1–6.5)	±0.05	1.8
5	10	6.4	(6.2–6.9)	±0.12	3.2
6	10	6.4	(6.3–6.6)	±0.06	1.6
7	22	6.5	(6.3–6.9)	±0.07	2.6

Males from Guadeloupe (samples 3 and 4) differed significantly in two measurements—zygomatic breadth and postorbital breadth. Female samples from the island were significantly different in these two measurements as well as mastoid breadth. On Jamaica, the three samples of males exhibited significant differences in greatest length of skull, zygomatic breadth, and length of maxillary toothrow. In greatest length of skull, samples 5 and 7 differed significantly from sample 6, whereas in zygomatic breadth, samples 6 and 7 differed significantly from sample 5. Female samples from Jamaica differed in greatest length of skull.

Interisland variation.—The seven samples from the three islands were compared for both sexes to determine if significant variation occurred among the samples and islands. All measurements for both sexes exhibited significant differences among the samples (Table 1). However, in only two measurements (mastoid breadth and postorbital constriction) did samples from one island form a subset significantly different from those of the other island. In both of these measurements,

the three samples of females from Jamaica formed a subset that did not overlap samples from Trinidad and Guadeloupe. The samples formed two to four overlapping subsets in all of the other measurements for both sexes.

Conclusions.—In any analysis of variation in *Molossus molossus,* the sexes must be considered separately. The analyses have shown that there is significant intraisland and interisland variation. The interisland variation, however, was of such a nature that the populations from the three islands cannot be distinguished on the basis of a single measurement. The degree of intraisland and interisland variation cannot be compared using these methods, but with significant variation present at both levels, multivariate analyses should be useful in making such comparisons.

Multivariate Analyses

Fig. 1 shows the results of the cluster analyses of the distance coefficients for males and females. The cluster analysis for females (cophenetic correlation coefficient, 89.1%) has the seven samples divided into three clusters which correspond to the three islands. The samples from Trinidad and Guadeloupe, although widely separated, are grouped more closely to each other than to the Jamaican samples. In the analysis for males (cophenetic correlation coefficient, 83.5%), the samples are also grouped into three clusters. However, in this analysis, sample 2 from Trinidad is grouped with the two samples from Guadeloupe. The remaining portions of the clusters are identical with those of the females.

Comparing the individual distance coefficients reveals some interesting results. Among the three samples on Jamaica the highest distance coefficient is 1.176 between male samples 5 and 6. The lowest coefficient is between female samples 5 and 7 (0.513). The distance coefficients between the two samples on Guadeloupe were 0.564 (females) and 0.668 (males) and on Trinidad were 0.622 (females) and 1.262 (males). These values, at least in some cases, are higher than would be expected of intraisland comparisons of populations of the same species; however, the interisland comparisons reveal values that are generally higher. The lowest distance coefficient among samples on Jamaica and Guadeloupe was 1.277 for males in samples 4 and 6 and among samples on Jamaica and Trinidad was 1.307 for females in samples 1 and 5. These low values for the interisland comparisons are higher than any of the intraisland comparisons. The lowest interisland value between Guadeloupe and Trinidad was 1.017 between female samples 2 and 4. This value is slightly lower than the intraisland value found for males on Trinidad (1.262).

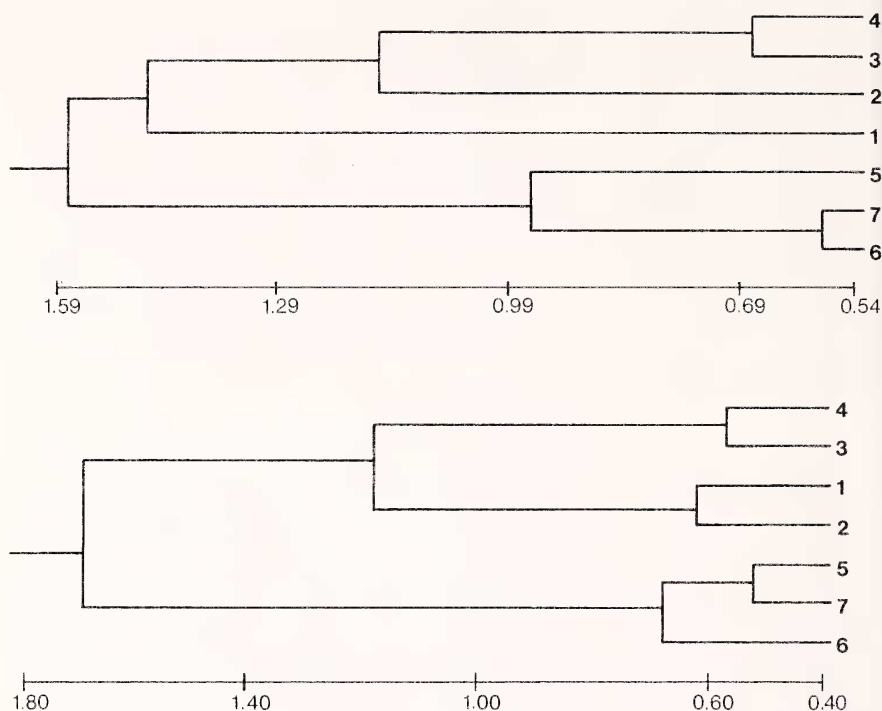The first three principal components extracted from the matrix of

Fig. 1.—Phenograms of numbered samples (see text for key to numbers) of *Molossus molossus* (males, top; females, bottom) from the Antilles computed from matrices based upon 10 characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for males is 83.5% and for females 89.1%.

correlation among characters are shown for males and females in Fig. 2. The percent of phenetic variation explained by the first three principal components for males and females, respectively, were 51.5 and 75.6 for component I, 28.1 and 13.5 for component II, and 12.5 and 5.5 for component III. Results of principal components analyses showing the influence of each character for the first three components are given in Table 2.

Most characters are heavily weighted in the first component for both sexes. However, rather low values were found for length of forearm, length of maxillary toothrow, and breadth across upper molars for males; length of mandibular toothrow is lowest for females. In component II, characters with heavy weighting in males were greatest length of skull, mastoid breadth, length of maxillary toothrow, and
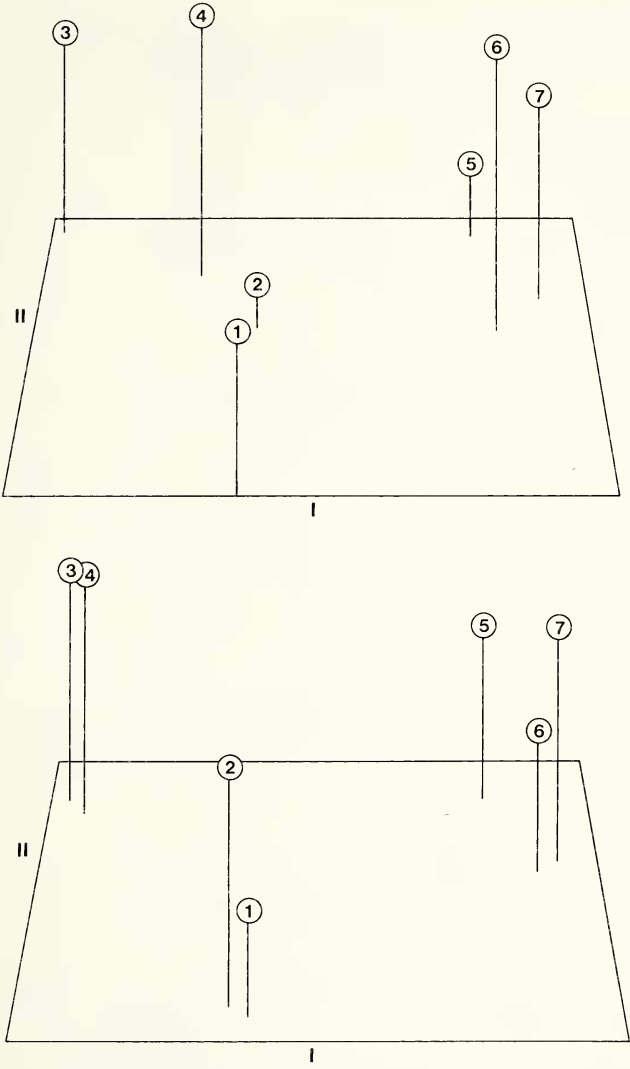
Fig. 2.—Three-dimensional projections of samples (see text for key to numbers) of *Molossus molossus* from the Antilles (males, top; females, bottom) onto the first three principal components based on matrices of correlation among one external and nine cranial measurements. Components I and II are indicated in the figure and component III is represented by height.

Table 2.—*Principal component loadings for 10 characters of* Molossus molossus.

Characters	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Length of forearm	0.379	−0.448	0.691	0.802	−0.566	−0.053
Greatest length of skull	0.758	−0.567	−0.272	0.962	0.078	0.178
Condylobasal length	0.872	0.106	−0.267	0.986	−0.035	−0.018
Zygomatic breadth	0.663	0.471	0.561	0.915	−0.325	0.177
Mastoid breadth	0.747	−0.601	0.207	0.876	−0.221	−0.036
Breadth of braincase	0.861	0.299	−0.407	0.738	0.360	−0.525
Postorbital breadth	0.986	0.040	0.107	0.970	−0.237	−0.030
Length of maxillary toothrow	0.309	0.839	0.242	0.723	0.597	−0.100
Breadth across upper molars	0.396	−0.814	−0.059	0.972	0.054	−0.058
Length of mandibular toothrow	0.842	0.487	−0.184	0.683	0.563	0.444

breadth across upper molars, and for females were length of forearm, length of maxillary toothrow, and length of mandibular toothrow. Length of forearm for males and breadth of braincase for females were the only characters weighting heavily in component III.

In both of the three-dimensional projections (Fig. 2), the intraisland groups appear to be grouped closer to each other than any interisland comparisons. The only possible exception would be samples 2 (Trinidad) and 4 (Guadeloupe) for males. The other intraisland groups are tightly clustered. In both sexes from Jamaica, samples 6 and 7 are closer to each other than either is to sample 5.

In both male and female *Molossus molossus*, multivariate analyses of variance showed that there were significant ($P < .0001$) morphological differences among geographic samples in the following tests: Hotelling-Lawley's Trace; Pillai's Trace; Wilk's Criterion; Roy's Maximum Root Criterion. Two-dimensional plots of the seven samples onto the first two canonical variates based on a matrix of variance-covariance among length of forearm and nine cranial characters are presented in Fig. 3. The percentages of phenetic variation represented in the first two canonical variates for males and females, respectively, were 60.1 and 84.5 for variate I and 22.5 and 9.8 for variate II.

Length of forearm in males (18.4%) and postorbital constriction in females (41.09%) contributed the most toward separating the samples on the first variate (Table 3). Other characters that contributed more than 10% on the first variate include postorbital constriction, mastoid breadth, greatest length of skull, and breadth across upper molars for males, and condylobasal length, zygomatic breadth, and length of forearm for females. Three characters in males contributed more than 10% to the separation on the second variate, namely, greatest length of skull, length of forearm and zygomatic breadth, whereas four characters in females (greatest length of skull, zygomatic breadth, condylobasal length, length of mandibular toothrow) contributed more than 10% to the separation on the second variate.

Examination of the two-dimensional plot for females reveals the three intraisland groups cluster together and show no interisland overlap. The three Jamaican samples and the two Trinidad samples are broadly overlapping. However, the means for the two samples from Guadeloupe fall outside of one standard deviation of the other sample.

Examination of the two-dimensional plot for males reveals the intraisland groups are not nearly as tightly clustered as was seen for females; however, no interisland samples were found to overlap. Sample 6, from Jamaica, is totally separated from all other samples studied. The other two Jamaican samples (5 and 7) do overlap, but the means are outside of one standard deviation. The one standard deviation ellipses for the two samples from Guadeloupe are just touching. The two

intraisland samples with the most overlap are from Trinidad; however, even here the means fall outside the one standard deviation ellipse of the other sample.

Discussion

Significant morphological differences can be demonstrated among samples of *M. molossus* that originate from geographic areas in close proximity on the same island. From collecting sites about 55 kilometers apart on Guadeloupe, two samples of males differed significantly in two measurements and the females in three. Among the three samples from Jamaica (total distance separating sample sites of 30 kilometers), males differed in three measurements and females in one. Interpretation of these results could indicate that taxonomic recognition be given to populations on a single island. Therefore, our first hypothesis—no significant differences among intraisland samples—is rejected.

The best methods for comparing intraisland and interisland variation in *Molossus molossus* are multivariate techniques, but no one analysis seemed better than another. Each analysis gave a slightly different view of the data. We would suggest that as many types of analyses as possible be used when studying morphometric variation in *Molossus molossus*.

In the cluster analyses of distance coefficients, the females formed three clusters corresponding to the islands. In males there were also three clusters, but one of the samples from Trinidad grouped with the samples from Guadeloupe. The intraisland distance coefficients are generally higher than would be expected for samples of other species from such close geographic proximity. However, the interisland values were generally higher than the intraisland comparisons. The one exception was between the samples of males on Trinidad, which would account for the grouping in the cluster analysis.

The samples of females form tight clusters based upon their island of origin in the principal component analysis. The males from Jamaica also form a tight cluster in the principal component analysis; however, the samples of males from Trinidad and Guadeloupe are fairly widely separated. It would be difficult to determine the geographic relationships of the samples from the latter two islands based only on study of Fig. 2.

The two former multivariate analyses give a picture of the relationships of the populations without weighting the characters; therefore, a canonical analysis weighting the characters was also conducted. The female samples again are closely clustered based upon their geographic origin, especially those from Jamaica and Trinidad. The two populations of females from Guadeloupe are somewhat more separated in this analysis than in the others. There is no interisland overlap and the
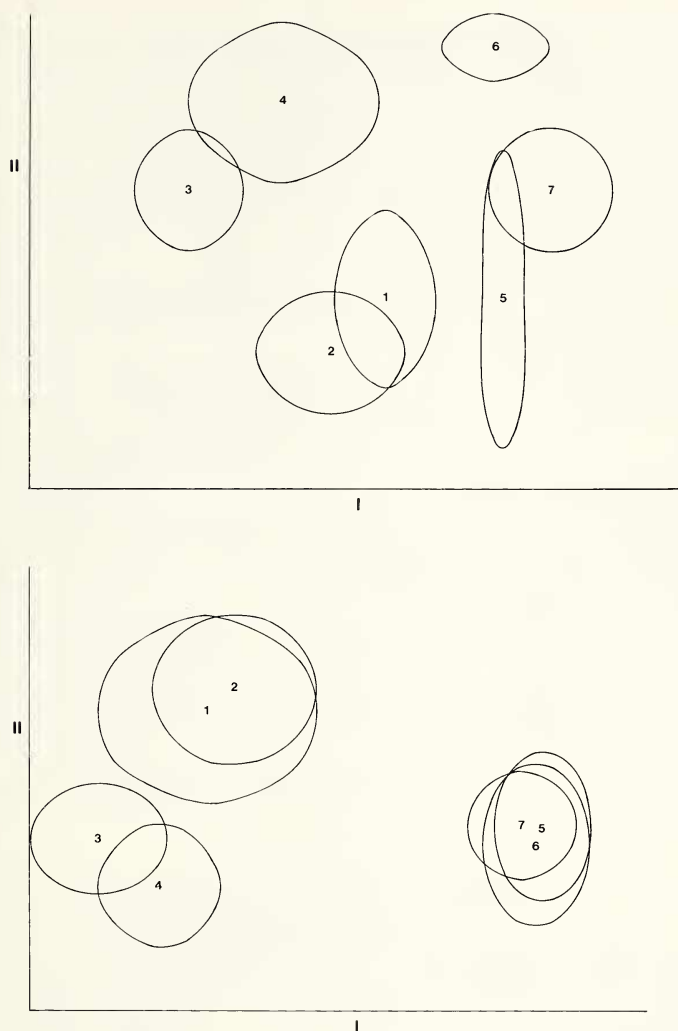
Fig. 3—Two-dimensional projections of samples (see text for key to numbers) of *Molossus molossus* from the Antilles onto the first two canonical variates based on a matrix of variance-covariance among one external and nine cranial measurements.

intraisland relationships are quite clear. For males the picture is quite different. The only overlap present is intraisland, but there is even little of this. The interisland relationships are not clear, particularly because of the isolated position of sample 6 from Jamaica.

Table 3.—*Eigenvalues of canonical variates showing the percentage influence among the one external and nine cranial characters of Molossus molossus.*

Characters	Males				Females			
	I		II		I		II	
	Normalized score	Percent influence	Normalized score	Percent influence	Normalized score	Percent influence	Normalized score	Percent influence
Length of forearm	-0.05412546	18.40	-0.11802628	24.24	-0.02285794	10.18	0.01896076	3.54
Greatest length of skull	0.08893837	13.54	0.28601946	26.31	0.02581785	4.96	-0.38688084	31.20
Condylobasal length	0.05589704	8.28	0.00171426	0.15	0.07652449	14.34	0.19524167	15.36
Zygomatic breadth	0.04423315	0.04	-0.29602578	16.98	-0.11002061	13.29	0.46939735	23.80
Mastoid breadth	0.14871458	13.65	-0.11420466	6.33	0.08500490	9.86	0.09280756	4.52
Breadth of braincase	0.06342258	4.92	0.19351566	9.06	-0.00999643	1.00	-0.04364188	1.82
Postorbital constriction	0.49822111	16.47	0.25092000	5.01	0.96659557	41.09	-0.05246146	0.94
Length of maxillary toothrow	-0.14342332	7.34	0.19524290	1.04	-0.03726515	2.45	-0.17354938	4.78
Breadth across upper molars	-0.16031757	10.98	0.10709512	4.43	-0.00042139	0.04	-0.09957419	3.69
Length of mandibular toothrow	0.11032667	6.38	0.18462909	6.45	0.03771688	2.79	-0.33335310	10.35

This study has shown that significant morphological variation can exist between intraisland populations of *Molossus molossus*. A similar type of study (Swanepoel and Genoways, 1978) of Antillean bats of the genus *Brachyphylla* did not reveal this level of intraisland variation. The current study has also demonstrated that patterns of geographic variation on a broader scale can be shown in *Molossus molossus* by using multivariate analyses. The local variation is more than would be expected in most other species of mammals (pocket gophers, especially *Thomomys*, are probably similar) but there are broader overriding patterns of geographic variation that exceed this local variation; therefore, the second hypothesis—interisland variation exceeds intraisland variation—can be accepted. Clearly, analyses of geographic variation can be performed on these small *Molossus*, but an understanding of local variation will aid in the appreciation of the broader geographic patterns.

The reasons this species has high levels of local geographic variation cannot be answered by the current study. Possibly as suggested by Jones et al. (1971), these local populations show a high degree of philopatry and inbreeding leading to morphological divergence on very local levels. We believe that genic analyses and ecological studies, particularly dealing with the breeding structure of these populations, would be very informative.

Specimens examined (200).—GUADELOUPE. Basse-Terre: 2 km N Ballif, 35; 1 km S Basse-Terre, 10. Grand-Terre: 1 km N, 1 km W St. François, 40. JAMAICA. St. Ann Parish: Queenhythe, 46; ½ mi S, ½ mi W Runaway Bay, 20. Trelawny Parish: Duanvale, 13. TRINIDAD. St. George Co.: Blanchisseuse, 6; Las Cuevas, 3; Maracas Valley, 10; Port-of-Spain, 7; San Rafael, 10.

LITERATURE CITED

GABRIEL, K. R. 1964. A procedure for testing the homogeneity of all sets of means in analysis of variance. Biometrics, 20:459–477.

GARDNER, A. L. 1966. A new subspecies of the Aztec mastiff bat, *Molossus aztecus* Saussure, from southern Mexico. Contrib. Sci., Los Angeles Co. Mus., 111:1–5.

HALL, E. R. 1981. The mammals of North America. John Wiley & Sons, New York, 1:xv + 1–600 + *90*.

HALL, E. R., AND K. R. KELSON. 1959. The mammals of North America. The Ronald Press Co., New York, 1:xxx + 1–546 + *79*.

HUSSON, A. H. 1978. The mammals of Suriname. Zool. Monogr., Rijksmuseum Nat. Hist., 2:xxiv + 1–569.

JONES, J. K., JR., J. D. SMITH, AND R. W. TURNER. 1971. Noteworthy records of bats from Nicaragua, with a checklist of the chiropteran fauna of the country. Occas. Papers Mus. Nat. Hist., Univ. Kansas, 2:1–35.

KOOPMAN, K. F. 1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. Amer. Mus. Novitates, 2651:1–33.

MILLER, G. S., JR. 1913. Notes on the bats of the genus Molossus. Proc. U.S. Nat. Mus., 46:85–92.

SCHMIDLY, D. J., AND F. S. HENDRICKS. 1976. Systematics of southern races of Ord's
    kangaroo rat, *Dipodomys ordii*. Bull. Southern California Acad. Sci., 75:225–237.
SERVICE, J. 1972. A user's guide to the Statistical Analysis System. Student Supplies
    Stores, North Carolina State Univ., Raleigh, 260 pp.
SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry: The principles and practice of sta-
    tistics in biological research. W. H. Freeman and Co., San Francisco, xiii +
    776 pp.
SWANEPOEL, P., AND H. H. GENOWAYS. 1978. Revision of the Antillean bats of the
    genus *Brachyphylla* (Mammalia: Phyllostomatidae). Bull. Carnegie Mus. Nat. Hist.,
    12:1–53.
VARONA, L. S. 1974. Catalogo de los mamiferos vivientes y extinguidos de las Antillas.
    Acad. Sci. Cuba, Habana, 139 pp.
YATES, T. L., AND D. J. SCHMIDLY. 1977. Systematics of *Scalopus aquaticus* (Lin-
    naeus) in Texas and adjacent states. Occas. Papers Mus., Texas Tech Univ., 45:
    1–36.